THE ABUNDANCE OF PLANTS BEARING EXTRAFLORAL NECTARIES IN COLORADO AND MOJAVE DESERT COMMUNITIES OF SOUTHERN CALIFORNIA

ROBERT W. PEMBERTON
Agricultural Research Service,
United States Department of Agriculture,
Rangeland Insect Laboratory, Montana State University,
Bozeman 59717

ABSTRACT

Measurements of the cover and frequency of EFN-bearing plants in seven warm desert communities in California revealed some of the highest levels of abundance of EFN-bearing plants that have been recorded for the temperate zone. The desert wash communities of both deserts had the highest covers (28 and 24%) and frequencies (0.27, 0.27) of EFN-bearing plants, whereas the sand dune communities had the lowest levels of abundance of EFN-bearing plants with covers of 2 and 0.0% and frequencies of 0.01 and 0.0. Colorado Desert communities had higher covers, frequencies, and numbers of EFN-bearing plants than Mojave Desert communities. The EFN antiherbivore defense system is predicted to be also common in other warm-dry communities of the world because those environments have an abundance of ants and plant groups, such as mimosoid legumes and cacti, known to have many EFN-bearing species. The EFN defense system may be particularly well suited to plants growing in warm-dry zones.

Extrafloral nectaries are nectar-secreting glands occurring most commonly on the vegetative parts of plants, but also at other sites such as developing fruit and the external parts of flowers. Instead of attracting pollinators, extrafloral nectaries (EFN's) have been shown to promote mutualistic interactions between plants and the insects, especially ants, that visit the EFN's. The insect participants gain sugars, amino acids, and water from the EFN's and benefit the plants by reducing the damage caused by the plant's herbivores (Janzen 1966, Bentley 1977a, Tilman 1978, Pickett and Clark 1979, Keeler 1980, Schemske 1980). At least 73 angiosperm families with almost 1000 species, and a few ferns have EFN's (Keeler 1979b). Plants with EFN's occur in most parts of the world (Zimmermann 1932, Schnell et al. 1963) and appear to be most common in the tropics (Bentley 1977b).

The abundance of EFN plants in plant communities has been examined in Costa Rica (Bentley 1976), Jamaica (Keeler 1979a), Nebraska (Keeler 1979b), Northern California (Keeler 1981a), Arizona (Keeler 1981b), and Hawaii (Keeler 1985). The cover of EFN plants has been found to be highest in the communities in Costa Rica (40–80%) and in the aspen (*Populus tremuloides* Michx.) dom-

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inated mountain forests of Arizona (39%). The lowest covers of EFN plants were in the Nebraska communities (0.0–8%) and in northern California where no EFN plants were found in the four communities sampled.

Zimmermann (1932) thought that xerophytes, as a rule, lacked EFN's and for this reason believed the dry floras of California to have practically no EFN plants. Except for *Helianthella californica* Gray (Keeler 1981a), no native EFN plants have been reported from California (Buckley 1982). After observing EFN's on cacti growing in California's deserts, I suspected that plants with EFN's were more abundant in California than was previously known. A greater abundance of plants with EFN's in California's deserts was also suggested by the abundance of ants (Wheeler and Wheeler 1973), which has been correlated with the abundance of EFN plants in other communities (Bentley 1976). The object of this study was to learn how abundant EFN plants might be in some California desert communities.

Methods

The abundance of EFN plants was determined by measuring their frequency and cover in four Colorado Desert and three Mojave Desert communities in southern California during March 1986. Frequency was determined by scoring the presence or absence of EFN plants at 1 m intervals along three 100 m transects through each community. Cover was determined by measuring to the nearest cm the linear distance occupied by EFN plants along each of the transects. Detection of EFN plants was made by direct observation of secreting EFN's on the plants, which was often aided by the presence of ants and other insects tending the nectaries. Locating EFN plants was made easier by examining species (and their relatives) previously reported to bear EFN's. The percentages of the floras with EFN plants in the areas studied was made by identifying the species, known to me, to have EFN in "Plants of Deep Canyon" (Zabriskie 1980), the area of the Colorado Desert transects, and in "A Flora of the Higher Ranges and Kelso Dunes of the Eastern Mojave Desert in California" (Thorne et al. 1981), the area of the Mojave Desert transects.

Colorado Desert Transects

The Colorado Desert transects were taken at the Phillip L. Boyd Deep Canyon Desert Research Center of the University of California. This area lies on the northeast slopes of the Santa Rosa Mountains and the adjacent southwest slopes of Coachella Valley, Riverside Co., California between 116°–117°W and 33°–34°N. The

Colorado Desert is the northwestern subsection of the Sonoran Desert, and is lower in altitude and more arboreal in character than the Mojave. Creosote bush scrub occupies the largest areas in both the Colorado and Mojave deserts (Munz and Keck 1959).

1. Creosote bush scrub—on rocky alluvial fan, west of the Channel of Deep Canyon Creek, 300 m elev. Common plants: *Encelia farinosa* A. Gray (Compositae), *Fouquieria splendens* Engelm. (Fouquieriaceae), *Larrea divaricata* Cav. (Zygophylaceae), and *Opuntia* spp. (Cactaceae).
2. Desert wash—sand and pebbles, Deep Canyon creek wash, 265 m elev. Common plants: *Acacia greggii* A. Gray and *Cercidium floridum* Benth. (Leguminosae), *Chilopsis linearis* (Cav.) Sweet (Bignoniaceae), and *Hyptis emoryi* Torr. (Labiatae).
3. *Yucca*-galleta grass—sand and rock hillside, adjacent to Hwy. 74 overlooking Deep Canyon, 820 m elev. Common plants: *Agave deserti* Engelm. and *Yucca schidigera* Roezl. ex Ortgies (Agavaceae), *Fouquieria splendens* and *Hilaria rigida* (Thurb.) Benth. ex Scribn. (Gramineae).
4. Sand dunes—Coachella Valley floor east of Thousand Palms, 40 m elev. Common plants: *Atriplex* spp. and *Salsola australis* R. Br. (Chenopodiaceae), *Larrea divaricata* and *Prosopis juliflora* (Sw.) DC. (Leguminosae).

Mojave Desert Transects

The Mojave Desert transects were located on the northern side of the Granite Mountains and at Kelso Dunes in San Bernardino Co., California at approximately 116°W and 35°N. The Mojave Desert is intermediate between the cold-temperate Great Basin Desert and the subtropical Colorado Desert (Turner 1982) and has a lower diversity of perennial plants than the Colorado Desert (Vasek and Barbour 1977). The average annual rainfall for the Mojave study areas is less than 200 mm (estimated from Thorne et al. 1981) and 90–150 mm for the Colorado Desert sites (estimated from I. P. Tinginan, unpublished booklet, "Natural History of Deep Canyon"). The average annual temperature for the Mojave sites is estimated to be around 26°C (Thorne et al. 1981) and higher for Deep Canyon, where it rarely freezes.

5. Sand dunes—eastern slope of Kelso Dunes, 900–1000 m elev. Common plants: *Astragalus* sp. (Leguminosae), *Croton californicus* Muell. Arg. (Euphorbiaceae), and various grasses.
6. Creosote bush scrub—sand and rock, alluvial fan, northern slope of the Granite Mts., 1250 m elev. Common plants: *Coleogyne ramosissima* Torr. (Rosaceae), *Eriogonum* spp. (Polygonaceae), *Larrea divaricata* and *Salazaria mexicana* Torr. (Labiatae), and *Yucca schidigera.*
7. Desert wash—boulders and sand, northern slope of Granite

Mts., 1350 m elev. Common plants: *Acacia greggii, Ephedra* sp. (Ephedraceae), *Isomeris arborea* Nutt. (Capparidaceae), *Prunus fasciculata* (Torr.) Gray (Rosaceae), and *Rhus trilobata* Nutt. ex T. & G. (Anacardiaceae).

Results

The plants observed to bear EFN's are listed in Table 1. All 11 species had active secreting EFN's in either the Colorado or Mojave Desert study areas, or both. The largest number of the species found to possess EFN's were cacti. The four *Opuntia* species had EFN's located on the areoles of the newly formed pads, flower buds, and flowers. The EFN's of *Ferocactus* were tubercules located above the areoles on the inside of the ring of flowers on top of the cacti. The EFN's of all cacti, except *O. acanthocarpa* Engelm. and Bigel., were tended by ants. The EFN's of *Chilopsis* were located on the leaf blades and were variable in their occurrence both within and between trees. The EFN's of ocotillo (*Fouquieria splendens*) were located on the flower buds, where relatively large 5 mm diameter drops of sweet tasting viscous nectar accumulated. *Acacia greggii* had small EFN's located on the leaves along the primary rachis between the branching secondary rachis bearing the leaflets. *Prosopis juliflora* bore EFN's on the rachis between the leaflets and also on the leaf petioles. Ants were tending its EFN's. The *Prunus* species had EFN's at the bases of their leaf blades. *Prunus fasciculata* had large numbers of small parasitic wasps (mainly Chalcidoidea) visiting its EFN's. In addition to the hymenoptera (ants and wasps) visiting the EFN's, lady beetles (*Hippodamia convergens* Guerin-Meneville) were observed on the EFN's of *Opuntia echinocarpa* Engelm. & Bigel. and small unidentified flies were observed feeding on the nectaries of *Chilopsis.*

The abundance of EFN plants in the different communities of the Colorado and Mojave deserts is shown in Table 2. The desert wash communities of both deserts had the highest covers (27.74%, 23.89%) and frequencies (0.277, 0.266) of EFN plants. The sand dune communities, with 1.36% and 0.0% covers, and 0.016 and 0.0 frequencies, had the lowest abundance of species with EFN's. The creosote bush scrub communities were intermediate in both deserts (cover 6.58%, 0.07%; frequency 0.120, 0.003). The communities of the Colorado Desert had, on average, a higher EFN plant cover ($\bar{x}$ = 9.8%) and frequency ($\bar{x}$ = 0.118) than those of the Mojave cover ($\bar{x}$ = 8.0%) and frequency ($\bar{x}$ = 0.090). The $\bar{x}$ number of EFN plant species was also higher in the Colorado communities with 3 vs. 1.66 species for the Mojave communities.

The percentages of species with EFN's in the native flora were 0.95% (1/105) for Kelso Dunes and 2.61% (10/382) for the Granite Mountains of the Mojave, and 3.20% (18/562) for Deep Canyon of the Colorado.

TABLE 1. PLANTS OBSERVED TO HAVE EXTRAFLORAL NECTARIES (EFN) AT THE COLORADO AND MOJAVE DESERT STUDY SITES. C = Colorado, M = Mojave. *Previously unreported EFN plant. [1]All species were observed to secrete nectar. [2]EFN's were observed on flower buds and bracts in May 1987, in southern Nevada and were visited by lady beetles.

Species	Desert	EFN site	Remarks[1]
Cactaceae			
Opuntia acanthocarpa Engelm. & Bigel.	C, M	areoles	Pickett and Clark 1979
**O. basilaris* Engelm. & Bigel.	C, M	areoles	ants tending
**O. bigelovii* Engelm.	C	areoles	ants tending
**O. echinocarpa* Engelm. & Bigel.	C, M	areoles	lady beetles and ants tending
Ferocactus acanthodes (Lem.) Britt. & Rose	C	above areoles	ants tending
Bignoniaceae			
**Chilopsis linearis* (Cav.) Sweet	C	leaf blade[2]	a few flies taking nectar
Fouquieriaceae			
**Fouquieria splendens* Engelm.	C	flower buds	
Leguminosae			
**Acacia greggii* Gray	C, M	leaf rachis	
Prosopis juliflora (Sw.) DC.	C	leaf rachis and petiole	ants tending
Rosaceae			
**Prunus fasciculata* (Torr.) Gray	M	leaf blade	misc. parasitic wasps foraging
**Prunus fremontii* Wats.	C	leaf blade	

TABLE 2. ABUNDANCE OF PLANTS WITH EXTRAFLORAL NECTARIES IN THE COLORADO AND MOJAVE DESERTS. Combined data for three 100 meter transects per community.

Community location	Frequency n/300 points	% cover n/300 meters	Number of EFN species
Colorado Desert			
1. Creosote bush scrub	0.120	6.58	6
Deep Canyon	36/300	19.7/300	
2. Desert wash	0.277	27.74	2
Deep Canyon	83/300	83.2/300	
3. Yucca agave galeta grass	0.060	3.65	3
Deep Canyon	18/300	10.9/300	
4. Sand dunes	0.016	1.36	1
Cocachella Valley	5/300	4.1/300	
Mojave Desert			
5. Sand dunes	0.000	0.00	0
Kelso	0/300	0/300	
6. Creosote bush scrub	0.003	0.07	1
Granite Mt.	1/300	0.2/300	
7. Desert wash	0.266	23.89	4
Granite Mts.	80/300	71.7/300	

DISCUSSION

The detection of cacti previously unreported to bear EFN was predicted by their occurrence in other cacti (Lloyd 1908, Pickett and Clark 1979). Similarly, many *Prunus* (Dorsey and Weiss 1920) and *Acacia* species (Delpino 1886) are known to bear EFN's. *Chilopsis* was suspected to have EFN's because most members of the Bignoniaceae have them (Elias 1983). Less expected were the EFN's in ocotillo (*Fouquieria splendens*) since few members of the Fouquieriaceae have them (Elias 1983).

Although the abundance of EFN plants in some of the desert communities of this study was quite high (24 and 28% cover), none approached the high levels (40–80%) measured in three dry tropical forest habitats in Costa Rica (Bentley 1976). More similar were the Jamaican lowland (Keeler 1979a) and Hawaiian *Acacia koa* Grey (Keeler 1985) communities with covers by EFN plants of 28 and 21%. Most temperate communities that have been measured have much lower abundances of EFN plants than found in this study. The exceptions are Arizona aspen forest (39%) and an Arizona Sonoran Desert community, found to have a cover of 22% (Keeler 1981b). The cover for that Arizona desert community is similar to the cover (24 and 28%) of desert washes measured in this study.

The only published accounts of the frequency of EFN species in floras are for Hawaii and Nebraska. Keeler (1979b, 1985) found 2.5% of the indigenous species in Nebraska to have EFN's and 1.5% of Hawaiian natives in Hawaii Volcano National Park to bear EFN's.

The figures for this study (0.95, 2.61, and 3.20%) are similar and noteworthy because most of the desert community EFN plant covers are much greater than in Nebraska and most of the Hawaiian communities sampled. These differences are explained by the presence of EFN's in species that are both abundant and of large stature, such as *Chilopsis, Acacia, Prosopis, Fouquieria,* and *Prunus.* High plant covers of EFN plants have been measured in other communities having few or single or large statured EFN plants, such as *Acacia koa* in Hawaii and *Populus tremuloides* in Arizona.

The desert plants in this study comprised some of the highest EFN plant covers that have been measured in the temperate zone communities. I predict that EFN plants are also common in many of the world's warm deserts and other hot dry biomes such as savanna and tropical scrub.

A number of the taxa found to bear EFN's in this study have dryland relatives that are known to bear EFN's. Delpino (1886) found that 172 of the 258 *Acacia* and 11 of the 15 *Prosopis* species he examined bore EFN's. Broughton (1981) found EFN's in all 42 species of Australian *Acacia* that she studied, including those from the interior desert areas which had formerly been thought to lack EFN's. EFN's also occur in *Acacia* species that are native to Central America (Janzen 1966), the Caribbean and South America (Keeler pers. comm.), Africa (Ross and Gordon-Gray 1966), and India (Bhattacharyya and Maheshwari 1971). EFN's are also common in species of other mimosoid genera such as *Mimosa, Albizia,* and *Leucaena* (Bhattacharyya and Maheshwari 1971) that are prominent members of the world's warm-dry floras. The prevalence of EFN's in species of cacti in the genera *Opuntia* and *Echinocactus* (Lloyd 1908), *Ferocactus* (Blom and Clark 1980, Ruffner and Clark 1986), and others native to both North America and South America, further support the probability of an abundance of EFN plants in the New World warm deserts and tropical scrub communities.

The general richness and abundance of ants in the world's desert and warm-dry communities also supports the prediction of high levels of abundance of EFN-bearing plants in those regions, as they did in the deserts of southern California.

The use of a water based antiherbivore defense system may appear to be an inappropriate strategy for arid land plants; however, growth and reproduction in warm desert plants usually occur only in periods of increased water availability. Since secretion in EFN's is most active in expanding foliage and reproductive structures (Bentley 1977b, and this study), EFN defense is used during periods of water availability. The greatest abundance of EFN-bearing plants in this study was desert washes, areas where plants have greater access to water.

Protection of new growth and reproductive tissues may be rela-

tively more important in desert plants, since the possibilities of regrowth of tissues lost to herbivores is restricted by limited water. The EFN defense may be particularly well suited to these arid land plants because the vulnerable tissues are protected as they are being produced. EFN defenses also have the advantage of being effective against both specialist and generalist insect herbivores, which is usually not the case for specific chemical defenses (Beattie 1985).

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